Modelling the long-term dynamics of populations and communities of trees in boreal forests based on competition for light and nitrogen

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Abstract

This paper describes an individual-based and spatially explicit model for computing the long-term succession of a population or community of trees and the turnover of carbon and nitrogen in a forested ecosystem. In the model ecosystem trees are located within a simulated plot in a grid of cells that are sufficiently small to contain not more than one tree. Each tree consists of five mass compartments (stem, branches, leaves/needles, coarse roots and fine roots) and has its own area, varying in time, for the acquisition of nitrogen. Each tree competes with its nearest neighbours for light and nitrogen; i.e. growth depends on the limitations on light or nitrogen.

The calculation of biomass production is based on the potential biomass increment, obtained by means of an integrating parameter for tree net primary production (NPP) in the form of the maximum possible biological productivity of the leaves/ needles. Growth under the limited light and soil nitrogen are calculated, and the smaller of the two is used as the realised growth. The total growth of each tree is allocated to different mass compartments using species-specific proportions related to the age of the tree. The litter cohorts are assumed to decompose to form a pool of soil organic matter (SOM) in a manner that is dependent on climatic conditions and the quality of the litter. The simulated plot has an explicit nitrogen–carbon balance based on the turnover of these in the ecosystem linked to the dynamics of organic matter in the soil. The model, which allows standard forest inventory data to be used as input, has been constructed using an object-oriented approach.

Comparison of the output of the model with growth and yield tables shows that the current model provides quite similar time courses for the main tree parameters (height, diameter, basal area, etc.) in the case of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula pendula*) throughout Finland (60–70°N).
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1. Introduction

The long-term dynamics of a forest ecosystem is controlled by the dynamics of tree populations or

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communities occupying the site as related to the regeneration, growth and mortality of trees and the turnover of organic matter and nutrients. Modelling of the long-term dynamics of a forest ecosystem clearly needs an approach which combines the dynamics of tree populations with mass dynamics representing the flow of energy and cycle of nutrients through the ecosystem (Ågren et al., 1991; Rolff and Ågren, 1999). This kind of integrated approach is especially necessary for modelling the long-term dynamics of mixed forests containing species with variable responses to their environment and coexisting species (Liu and Ashton, 1995; Bartelink, 1998; Kolström, 1999).

Nitrogen dynamics will be of primary importance in the case of boreal forests, on account of the large impact on the overall productivity of the ecosystem (Ryan et al., 1996). Furthermore, the availability of nitrogen affects the allocation of overall productivity to individual trees, with a consequent differentiation in tree growth and size (Chertov, 1990). Size differentiation may further be enhanced by the availability of light, which is determined by the canopy position of each tree.

The interaction between the availability of nitrogen and light, both of which affect growth, is one of the main factors determining the dynamics of tree species composition and size structure of tree populations and communities under boreal conditions (Kellomäki and Kolström, 1994). This implies that there is competition for light and nitrogen between species and between individuals (within species) in relation to the spatial variation in the availability of these at the site and the positions of the trees relative to each other.

The family of gap models represents a popular way of modelling the long-term dynamics of multi-species tree communities (Botkin et al., 1972; Shugart, 1984). Regarding the differentiation of growth among trees, a common feature of gap models is that they scale the potential growth in relation to light, nitrogen and soil moisture. Potential growth is defined as the mean growth when there is no limitation on any resource. In some gap models the potential growth is equal to the maximum radial growth ever observed for a particular tree species (Weishampel and Urban, 1996). One approach that comes close to this is that presented by Chertov et al. (1999a,b), who introduced the concept of maximum biological needle or leaf productivity.

This indicates the maximum growth in mass per unit foliage mass (gram of mass per gram of foliage), and provides a concept that links the growth of single trees to the net primary production (NPP) of the ecosystem, which is allocated to trees through competition for light and nitrogen. On the other hand, maximum biological productivity may be linked to climate through temperature conditions by means of a similar scaling procedure, as is commonly done in many gap models (Chertov et al., 1999a,b).

In gap models, the availability of light is related to the properties of tree crowns and the size differences between trees; i.e. larger trees are assumed to shade smaller ones and the same mass of needles is assumed to cause more shading than of leaves, given a homogeneous distribution of the foliage mass in the canopy and an attenuation of the light that obeys the Beer–Lambert's law. This approach is simple, but it normally satisfies the needs of gap models as regards other assumptions that lie behind them. Only in few cases is spatial variability in light included (Urban et al., 1991; Weishampel and Urban, 1996), but this provides no fundamental benefits when studying the long-term dynamics of a forest ecosystem by means of such models.

Spatial and temporal variability in soil nitrogen is also excluded from gap models, and nitrogen is assumed to be distributed evenly in the soil so that it can be treated as a site-specific parameter. Furthermore, each tree has the same access to nitrogen, with the implication that competition for nitrogen is excluded in terms of the increasing area required around trees for nitrogen acquisition along with their growth in size and increasing need for nitrogen. The effects of the dynamics of nitrogen acquisition on competition for nitrogen and consequent growth are still poorly known, and have to date been ignored completely when the modelling the long-term dynamics of forest ecosystems.

We describe in this paper a model of the above kind which sets out from the potential NPP of the forest ecosystem in terms of its maximum biological productivity. This is allocated to individual trees through competition for light and nitrogen, the tree populations or communities occupying the site being treated as a set of separate trees with spatially explicit positions and entering into local interactions with a set of neighbouring trees defined by rules for the allocation

of light and available soil nitrogen. The model is parameterised for Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula pendula*) and validated against the results of growth and yield studies over the whole range of variability in site fertility throughout Finland (60–70°N).

2. Description of the model

2.1. Outlines

The model is an individual-based and spatially explicit combining the tree growth and soil processes within the concept of a single plant ecosystem (Chertov, 1983a). Biomass production is based on calculation of the potential biomass increment using the integrating parameter of tree NPP, in the form of the maximum possible biological productivity of the leaves/needles (Fig. 1).

The response of a tree to soil nutrient supply is considered in term of its specific consumption of nutrients, i.e. the amount of a given element necessary

for the synthesis of a unit of tree biomass as a species-specific parameter (Chertov, 1983a,b). Since the increment in tree biomass is also dependent on the within-stand light and nitrogen conditions, growth under the limited light and soil nitrogen is calculated and the smaller of the two is used to represent the realised growth (Liebig, 1843). The total tree increment is allocated to different compartments using species-specific proportions defined separately for three age statuses of the tree (young, middle-aged and old). The different cohorts of tree litter (leaves, roots and branches) are calculated for each tree in terms of the total mass and nitrogen content of each cohort, and are assumed to decompose in a manner dependent on climatic conditions and the nitrogen and ash content of litter (Chertov and Komarov, 1997). When a tree dies, an additional cohort of dead wood and coarse roots is included in the soil model.

2.2. Initialisation

In the initialisation of the model run, the location (co-ordinates) and type of the site are first defined. Consequently, the algorithm selects the weather station closest to the selected site, and the monthly temperature and precipitation statistics for this station are used in the calculations (Fig. 2). Furthermore, the initial values of soil properties (soil organic matter (SOM), nitrogen, water holding capacity) representing the type of the selected site are defined. The data files for the soil properties are available for the three parallel series of site types representing southern, middle and northern boreal vegetation zones covering more than 90% of the unplanned forest soils in Finland between 60° and 70°N. When initialising the soil parameters, it is also possible to use the values at the end of the previous rotation as an input if necessary.

In the second phase of the intiliasation, the properties of the tree populations to be occupying or occupying the stand are defined in terms of stand density per tree species and the distribution (mean value with standard deviation) of diameter, height and age of trees. The location of each trees is determined randomly, as also done if new trees are introduced during the course of simulation. One (pure stand) or several (mixed stand) tree species can occupy the stand at the same time with the definition of the properties of trees
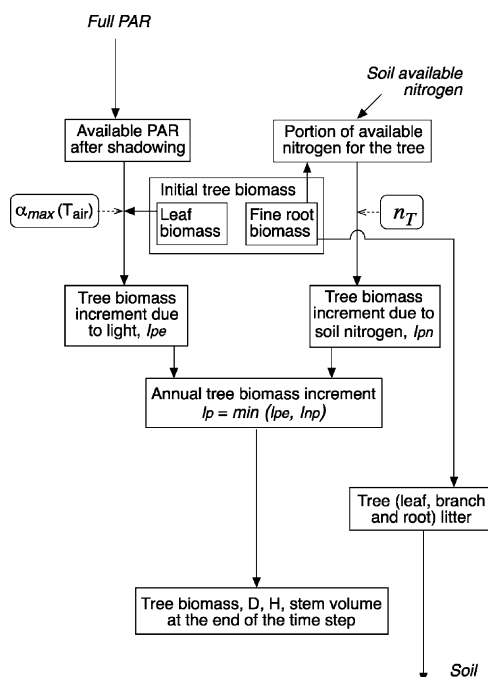

Fig. 1. Outlines of the model representing the main links between tree growth and environment.
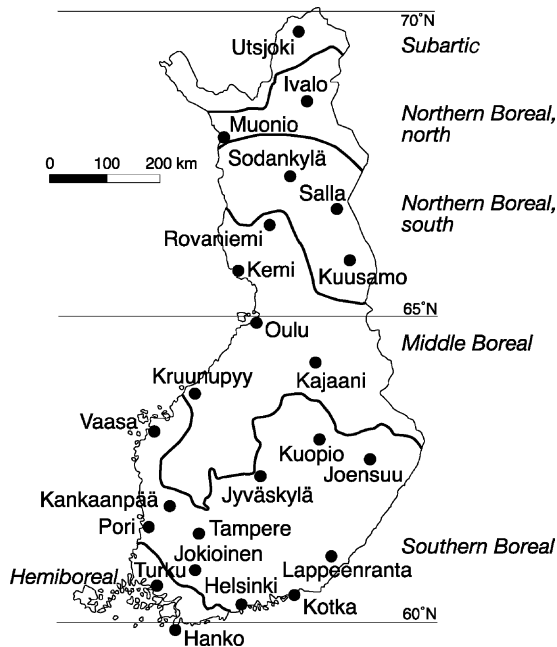
Fig. 2. Location of weather stations (dots) and the vegetation zones used to distinguish the parallel site types referred to when defining site fertility.

separately for each tree species. The inital values for the mass components of trees (stem, branches, leaves/needles, coarse roots and fine roots) are calculated from Eq. (1), employing the parameter values presented by Marklund (1988) for Scots pine, Norway spruce and birch:

$$W_d = \exp\left[b_0 + \left(\frac{b_1 D}{D + g}\right) + b_2 H + b_3 \ln H\right] \qquad (1)$$

where W_d is the dry weight of the tree compartment (kg), D the diameter at breast height (cm), H the height (m), and $b_0, \ldots, b_3$ and g are species-specific coefficients. The proportion of fine roots is assumed to be 10% of the total mass of root systems calculated on the basis of Eq. (1) and that of coarse roots 90%.

2.3. Calculating the total biomass growth and its allocation to mass components of trees

The tree structure used in the model consists of five compartments of dry mass (kg), i.e. leaf/needle B_l, branches B_{br}, stem B_{st}, coarse roots B_{cr} and fine roots B_{rf}. The total biomass of the tree, B_T, is the sum of

these five compartments. Let I_p be the total tree increment (kg per year) and L_p the total tree litter (kg per year). Consequently, the main balance equation with a time step $\Delta t = 1$ year is

$$\frac{\Delta B_T}{\Delta t} = I_p - L_p \qquad (2)$$

The total growth of the tree I_p is calculated as

$$I_p = \min\{I_{pe}(\alpha_{max}(T_{air}, PAR, B_l));$$
$$I_{pn}(n_T, N_m(B_{rf}, T_{soil}, W_{soil}))\} \qquad (3)$$

where I_{pe} is the tree increment based on the maximal biological productivity $\alpha_{max}(T_{air})$ depending on climatic conditions, the fraction of light available (PAR) for the tree and B_l the leaf biomass. Correspondingly, I_{pn} is the tree increment due to specific nitrogen consumption n_T, fine root biomass and $N_m(B_{rf}, T_{soil}, W_{soil})$ available soil nitrogen. The increment I_{pe} is calculated as

$$I_{pe} = \alpha_{max}(T_{air}) B_l K_{SH}(PAR) \qquad (4)$$

where $K_{SH}(PAR)$ $(0 \le K_{SH}(PAR) \le 1)$ is the light response multiplier. Correspondingly, the increment I_{pn} is defined as

$$I_{pn}(n_T, N_m(B_{rf}, T_{soil}, W_{soil}))$$
$$= \frac{N_m(B_{rf}, T_{soil}, W_{soil}) + N_{buffer}}{n_T} \qquad (5)$$

where $N_m(B_{rf}, T_{soil}, W_{soil})$ is available nitrogen originating from the area occupied by the tree at the current moment, and n_T is the specific consumption of nitrogen, a constant for each tree species. N_{buffer} consists of the nitrogen resorbed from senescent leaves and deposited from atmosphere for the use of the tree (Vitousek, 1982; Aerts, 1996; Killingbeck, 1996). When the total tree increment has been calculated, it is allocated to the different tree compartments using proportions specific to the tree species and age (Table 1).

Maximal biological productivity of a leaf/needle $\alpha_{max}(T_{air})$ (grams of biomass increment per gram of leaf/needle per year) indicates the maximal tree growth for each given set of climatic conditions with no limitations due to shading, soil moisture or nitrogen. The values of $\alpha_{max}(T_{air})$ are given as functions of the temperature sum (+5 °C threshold, degree-days, DD) based on Karpov (1969), Alexeev (1975), Chertov (1983b) and Kostin (1997) (Fig. 3):

Table 1
Distribution of biomass increment by compartments in relation to the age status of the tree[a]

Species	Age (years)	Stem α_s	Foliage α_l	Branches α_b	Coarse roots α_{cr}	Fine roots α_{fr}
Scots pine	<30	0.41	0.27	0.09	0.08	0.15
	31–130	0.38	0.30	0.09	0.09	0.14
	>130	0.30	0.30	0.08	0.08	0.24
Norway spruce	<30	0.30	0.38	0.12	0.05	0.15
	31–100	0.35	0.37	0.11	0.04	0.13
	>100	0.26	0.33	0.04	0.04	0.33
Birch	<20	0.30	0.44	0.07	0.04	0.15
	21–70	0.40	0.40	0.05	0.05	0.10
	>70	0.30	0.38	0.04	0.06	0.22

[a] Fraction of the total growth of tree.

- Scots pine:

$$\alpha_{max}(T_{air}) = 0.854 + 0.0016 DD - 0.00000076 (DD)^2$$
if $500 < DD < 3500$ \hfill (6)

- Norway spruce:

$$\alpha_{max}(T_{air}) = 0.623 + 0.0012 DD - 0.00000019 (DD)^2$$
if $700 < DD < 3000$ \hfill (7)

- Birch:

$$\alpha_{max}(T_{air}) = 1.745 + 0.0039 DD - 0.00000019 (DD)^2$$
if $500 < DD < 2500$ \hfill (8)

The specific consumption of nitrogen is the amount of nitrogen needed for the synthesis of a unit of biomass in each compartment; i.e. n_s for the stem,
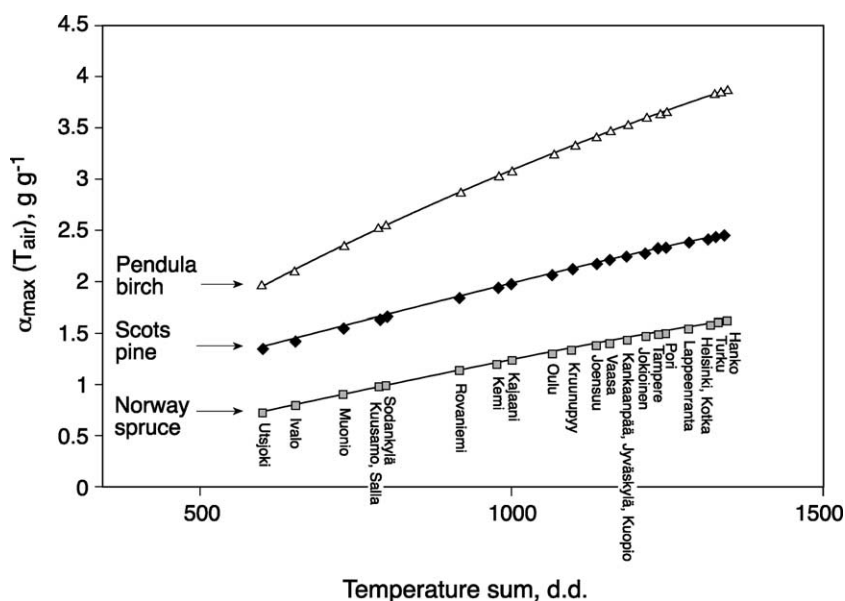

Fig. 3. Dependence of the parameter $\alpha_{max}(T_{air})$ on the temperature sum for Scots pine, Norway spruce and Pendula birch. The words on the line for Norway spruce are referring to the weather stations presented in Fig. 2. The weather stations form a south–north gradient of temperature sum from the latitude 60°N (Helsinki) to 70°N (Utsjoki). The weather station at Rovaviemi is at the artic circle (66°N).

Table 2
Specific consumption of soil nitrogen, n_i (kg N kg^{-1} tree increment) for different tree species and compartments

Tree species	Stem n_s (kg kg^{-1})	Leaves (needles) n_1 (kg kg^{-1})	Branches n_b (kg kg^{-1})	Coarse roots n_{cr} (kg kg^{-1})	Fine roots n_{fr} (kg kg^{-1})
Scots pine	0.0014	0.0060	0.0040	0.0024	0.0047
Norway spruce	0.0022	0.0100	0.0050	0.0030	0.0055
Birch	0.0015	0.0200	0.0040	0.0045	0.0100

n_1 for the leaves/needles, n_b for the branches, n_{cr} for the coarse roots and n_{fr} for the fine roots. The total specific consumption of nitrogen n_T is calculated as a weighted sum of these. Let $I_s = \alpha_s I_p$ (increment in stem), $I_1 = \alpha_1 I_p$ (increment in needles/leaves), $I_b = \alpha_b I_p$ (increment in branches), $I_{cr} = \alpha_{cr} I_p$ (increment in coarse roots) and $I_{fr} = \alpha_{fr} I_p$ (increment in fine roots), where I_p is the total mass increment and α_s, α_1, α_b, α_{cr}, α_{fr} are the specific consumption of nitrogen in growth of different mass compartments. The corresponding fractions of the mass increment reallocated between compartments:

$$n_T = n_s I_s + n_1 I_1 + n_b I_b + n_{cr} I_c + n_{fr} I_{fr}$$
$$= (n_s \alpha_s + n_1 \alpha_1 + n_b \alpha_b + n_{cr} \alpha_{cr} + n_{fr} \alpha_{fr}) I_p \qquad (9)$$

The values of n_T were calculated for each tree species based on Kazimirov et al. (1977, 1978), Mälkönen (1974, 1977) and Kubin (1983) (Table 2).

2.4. Calculation of the impact of competition on light and nitrogen

When calculating the availability of light and nitrogen, the plot is split into a grid of cells of size 50 cm × 50 cm, assumed to be small enough to contain only one tree per cell. This grid is used to calculate the shadowing area of each tree and a zone of available for the acquisition of nitrogen; i.e. an expanding set of neighbouring cells as determined by the size of the tree. Litter and humus as sources of nitrogen are assumed to be distributed homogeneously among the cells.

Calculation of the *competition for light* is based on the shadows cast by neigbouring trees on each tree under the assumption that light comes from the zenith. Each tree creates a shadow zone S_i, which is a quadrat of size R_i located at the centre of cell x_i. The extent of shadowing S_i is dependent on the height of the tree.

The tree in cell x_i casts a shadow on the neighbouring tree x_j if the shadow zone S_i covers the cell x_j and if the ratio of the height H_i of the tree x_i to the height H_j of the tree x_j is greater than a fixed value β, i.e. $H_i/H_j > \beta$. Symmetric shadowing occurs when two trees shadow each other. The contribution of a given tree to the shadow formed by all trees shadowing one cell is assumed to be additive in relation to the value of the shadow coefficient $0 \leq K_E \leq 1$ for the tree x_i:

$$K_E(x_i) = 1 - \sum S_1 k_1 \qquad (10)$$

The species-specific parameter S_1 indicates the fraction of light intercepted by the crown of the shadowing tree and k_1 the number of trees of a given species shadowing the tree x_i. The values of S_1 are 0.11 for Scots pine and birch and 0.13 for Norway spruce (Tselniker, 1978).

The impact of competition for light on growth is introduced through the light response multiplier $K_{SH}(PAR)$, which indicates the fraction of the light above the canopy available to a given tree. The values of K_{SH} are assumed to be linearly related to K_E for Scots pine and birch, which are shadow-intolerant species, and non-linearly for Norway spruce, a shade-tolerant species (Alexeev, 1975; Tselniker, 1978):

$$K_{SH} = \beta K_E \qquad (11)$$
$$K_{SH} = 1 + 0.44 \log K_E \qquad (12)$$

When calculating the *competition for nitrogen* it is assumed that each tree has a nutrition zone around it and that it can intercept all the available nitrogen from this zone for growth. The soil nitrogen zone for an individual tree, Z_i, is modelled by a "pseudo-disc" (a square in the present model) $Z_i = b(x_i, R_i)$, where x_i is the centre of cell and R_i is the radius of the zone. The size of cell expands in a discrete manner in relation to the increase in the diameter of the tree, with an

increasing number of adjacent cells coming to be included in the nitrogen zone of the given tree.

If there is no overlapping of the nitrogen zone of a given tree, x_i, with that of any of its neighbours, then all the nitrogen available within the zone will used for its nutrition, and the total amount of nitrogen consumed by it will be the sum of available nitrogen in all the cells belonging to its nitrogen zone. If the zone of the tree x_i overlaps with that of another tree x_j, then the available nitrogen within the intersection zone has to be divided between the competing trees in proportion to the mass of their fine roots. The fine roots are assumed to be distributed homogeneously over the nutrition zone of a tree; i.e. their mass in a given cell is calculated by dividing the total mass of fine roots of the tree by the number of cells in its nutrition zone.

2.5. Conversion of biomass to dendrometric characteristics

The model calculates the biomass of the stem, which is converted to diameter and height measurements. Let D' be the derivative of Eq. (1) for the diameter (D), H' the derivative for the height (H) and ΔW_{ds} the increment in stem mass:

$$\Delta W_{ds} = D'\Delta D + H'\Delta H \tag{13}$$

Since $\Delta H = k\Delta D$, we have:

$$\Delta D = \frac{\Delta W_{ds}}{D' + kH'} \tag{14}$$

In order to determine the diameter and height of the tree, it is assumed that it will retain its form:

$$k = \chi\frac{H}{D} \tag{15}$$

The values of the parameter χ are species-specific and are affected by the limitation of growth by the availability of light and nitrogen (Table 3). This implies

Table 3
Values of χ for different tree species under light and nitrogen limitation

Tree species	Light limitation	Nitrogen limitation
Scots pine	0.90	0.70
Norway spruce	0.95	0.80
Birch	1.15	0.85

that under conditions of light limitation, the tree will grow in height more than in diameter in relative terms. Similarly, given an ample supply of nitrogen, the radial growth will be relatively larger than the height growth.

2.6. Mortality and the decomposition of litter and humus

Mortality of trees may be represented as a combination of two process; i.e. the capacity of a tree to support its total mass (resource-based mortality) and its probability of death as a function of increasing age (random mortality). The resource-based mortality utilises the approach where the current ratio $r_c(t)$ between the leaf mass $B_l(t)$ and the total tree mass $B_T(t)$ is compared with the threshold values of the same ratio $r(t)$ with an assumption that if $r_c(t) < r(t)$, the tree will die in 3 years. The threshold values of $r(t)$ are calculated as a function of the total mass of the tree (B_T):

$$r(t) = g_1 - g_2 \ln B_T(t) \tag{16}$$

where g_1 and g_2 are species-specific parameters with values evaluated after the model calibration to match the mortality to meet that obtained from growth and yield tables. The values for g_1 and g_2 are 0.09 and 0.03 for Scots pine and Norway spruce, and 0.14 and 0.07 for Pendula birch, respectively.

The dead trees are added to the litter deposited on the soil, which also includes the litter from other mass compartments. The annual amount of litter from different mass compartments is a given fraction of the annual masses of the compartments, 0.0025 for branches and coarse roots and 1.0 for fine roots. This part is also equal to one for the foliage litter from deciduous species, whereas it is 0.25 and 0.15, for Scots pine and Norway spruce (Kazimirov and Morozova, 1973; Kazimirov et al., 1977; Mälkönen, 1974, 1977; Kubin, 1983), respectively. The nitrogen content of litter is a species-specific parameter having the values given in Table 4. This is used for calculating the amount in nitrogen contained in organic matter in the soil and eventually for determining the amount released annually.

The model developed by Chertov and Komarov (1997) is used for analysing the decomposition of litter and humus SOM. This presupposes one pool

Table 4
Nitrogen content (kg kg^{-1} litter) of litter from different tree species and compartments

Tree species	Stem	Foliage	Branches	Coarse roots	Fine roots
Scots pine	0.0014	0.0030	0.0040	0.0024	0.0047
Norway spruce	0.0022	0.0050	0.0050	0.0030	0.0055
Birch	0.0015	0.0010	0.0040	0.0045	0.0100

for litter and three for SOM, i.e. undecomposed litter, partly humified organic material (forest floor and peat) and humus bound in the mineral matrix of the topsoil. Litter is assumed to be transformed to humus by the soil fauna, and SOM is assumed to be mineralised by micro-organisms, the rates of these processes being determined by soil temperature and moisture and the nitrogen and ash content of the litter. With the decomposition of SOM, nitrogen is released and made available for growth. The degree of nitrogen retention in the decomposing material is a function of the nitrogen content of the litter and the current nitrogen content of the forest floor (Chertov, 1990). The immobilisation of nitrogen in the mineral topsoil is a function of the carbon/nitrogen ratio in the humus. Nitrogen input from the atmosphere is taken into account, but not

biological fixation. Nitrogen losses through leaching, for example, are not directly considered in the present version of the model. For further details of the soil model, see Chertov et al. (1999c, 2001).

3. Validation of the model

The main focus in validation was on comparing the simulated density, height and diameter, basal area and volume of a given tree stand with measured data from the Finnish National Forest Inventory, covering the whole of Finland. Furthermore, the simulated values were compared with ones obtained from growth and yield tables (Koivisto, 1962), too. The initial stands were 5-year-old pure ones on *Myrtillus* site representing: (i) pine with height 1.2 m and density 9000 trees ha^{-1}; (ii) spruce with height 1.0 m and density 9000 trees ha^{-1} and (iii) birch with height 1.6 m, diameter 1.0 cm and density 9000 trees ha^{-1}.

In the growing stand, the number of trees reduced well in line with the pattern obtained from the growth and yield tables (Fig. 4). Mortality turned out not to be sensitive to the changes in the parameter values (g_1 and g_2) in the mortality function; i.e. an increase of 10% in the values led to a 6 % increase in mortality for
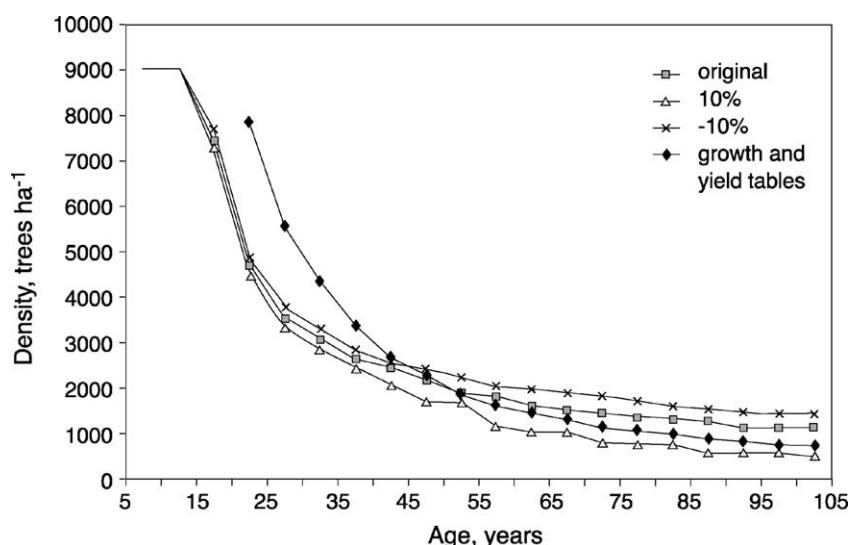

Fig. 4. Density of a Scots pine on a *Myrtillus* site in southern Finland as a function of stand age and the sensitivity of stand density to changes in the values of the main parameter in the mortality model as compared to the values obtained from growth and yield tables (Koivisto, 1962). The inital stand approximates that behind the growth and yield tables.
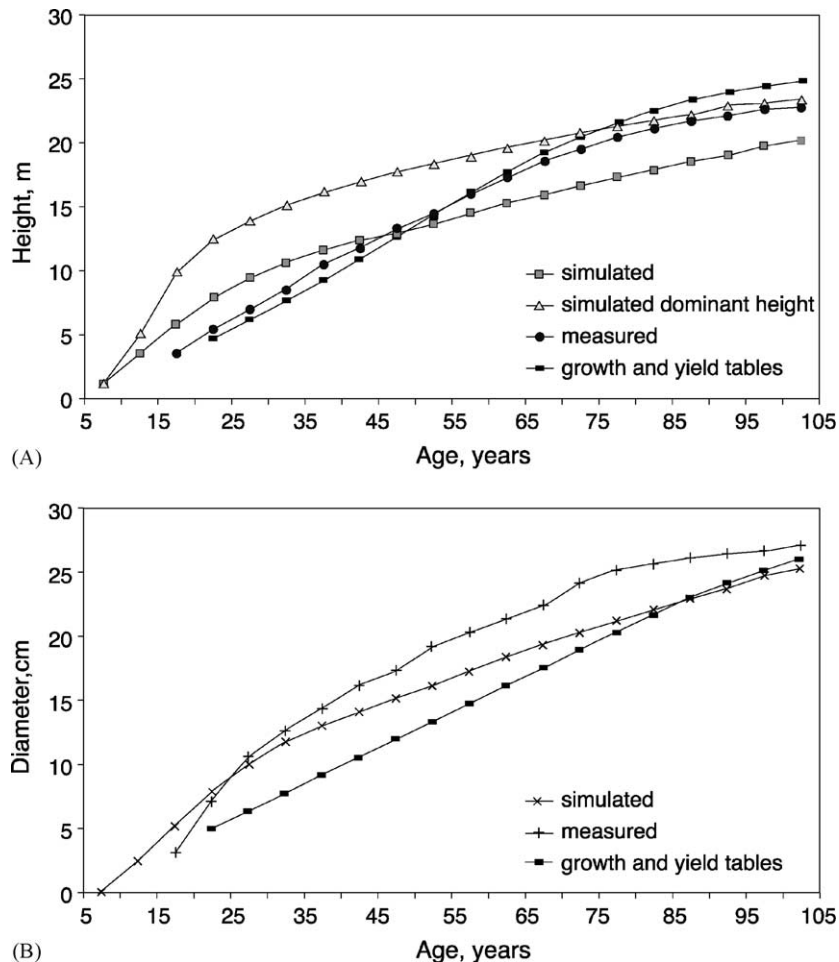
Fig. 5. Development of (A) height and dominant height, and (B) diameter of trees in a Scots pine stand on a *Myrtillus* site in southern Finland, and comparison with growth and yield tables (Koivisto, 1962) and the values computed on the basis of trees on the permanent sample plot of the Finnish National Forest Inventory (measured).

pine, and a reduction of 10% to a 4% decrease in mortality (the corresponding figures for spruce being +3 and −2%, and those for birch +4 and 0%, respectively).

Regarding height, the resemblance between the simulated and measured data was quite good in all cases. The height development was overestimated at the beginning of the simulation (Fig. 5), but this difference disappeared after year 45 in the Scots pine stands and after year 50 in the birch stands. In the case of the Norway spruce stands, the simulation overestimated the height development throughout the rotation. The simulated values for the dominant height in each tree species

(mean height of the 100 thickest trees ha^{-1}) correlated very closely with those obtained from the growth and yield tables. The pattern of diameter growth was close enough to the measured values throughout.

The overall development of the population or community of trees is well indicated by the trends in basal area and volume of trees as affected by the mortality and growth of the trees (Fig. 6). The temporal pattern in terms of basal area for Scots pine was similar to that obtained from the growth and yield tables, but the simulated values were clearly higher. Nevertheless, the volume of trees (stocking) was very similar to that obtained from the growth and yield tables, although it
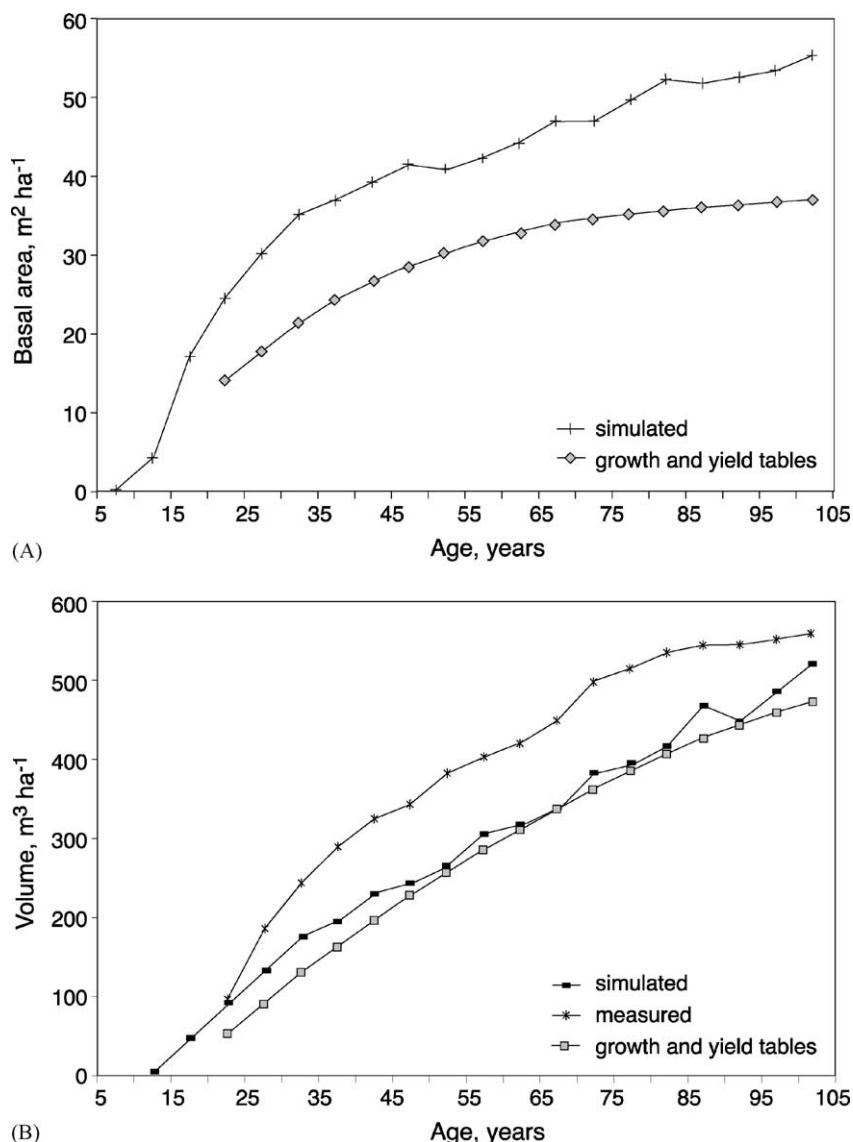
Fig. 6. Development of (A) basal area, and (B) volume in a Scots pine stand on a *Myrtillus* site in southern Finland, and comparison with growth and yield tables (Koivisto, 1962) and the values computed on the basis of trees on the permanent sample plot of the Finnish National Forest Inventory (measured).

remained lower than that calculated from data from the Finnish National Forest Inventory.

4. Performance of the model

The influence of stand density was studied by comparing the biomass production of Scots pine stands of densities 1000, 2500 and 5000 trees ha^{-1} with the age of 5 years and the mean height 1.2 m, representing *Oxalis–Myrtillus*, *Myrtillus* and *Calluna* site types, respectively. Table 5 shows that the higher the density, the higher was the total biomass production. Furthermore, the amount of "living" biomass in a stand did not differ with density, but mortality was higher at higher densities. Similarly, the more fertile

Table 5
Effect of site fertility and spacing on the growth and mortality of Scots pine in southern Finland

Site and spacing (ha^{-1})	Stocking (Mg ha^{-1})	Mortality (Mg ha^{-1})	Total production (Mg ha^{-1})
Oxalis–Myrtillus			
1000 Stems	409	34	443
2500 Stems	390	103	493
5000 Stems	401	116	517
Myrtillus			
1000 Stems	317	26	342
2500 Stems	308	73	381
5000 Stems	296	107	403
Calluna			
1000 Stems	169	13	181
2500 Stems	157	45	202
5000 Stems	148	69	216

Table 6
Timber production in an unmanaged spruce–birch stand on a *Myrtillus* site in southern Finland

Timber assortment	Norway spruce	Birch
Commercial timber (m^3 ha^{-1})		
Pulp wood	42	34
Saw timber	56	96
Total timber	98	129
Logging residuals (Mg ha^{-1})	18	20
Grand total (Mg ha^{-1})	116	149

A mixed spruce–birch stand was used as an example of the growth of mixed stands and their biomass, height and diameter development, the effect of felling on stand development and changes in carbon and nitrogen reserves in the soil. The initial stand was 5 years old with 2080 spruce and 4000 birch ha^{-1}, the mean height and diameter for spruce being 1.2 m and 1 cm and for birch 1.6 m and 1 cm.

Two runs were done in order to demonstrate the performance of this initial tree community. The first run represented no thinning with the terminal cut at the

the site was, the higher were both "living" biomass and mortality; i.e. the total biomass production was highest on the *Oxalis–Myrtillus* site, about 517 Mg ha^{-1}, and the lowest on the *Calluna* site, about 181 Mg ha^{-1}.

Table 7
Timber production in a managed spruce–birch stand on a *Myrtillus* site in southern Finland

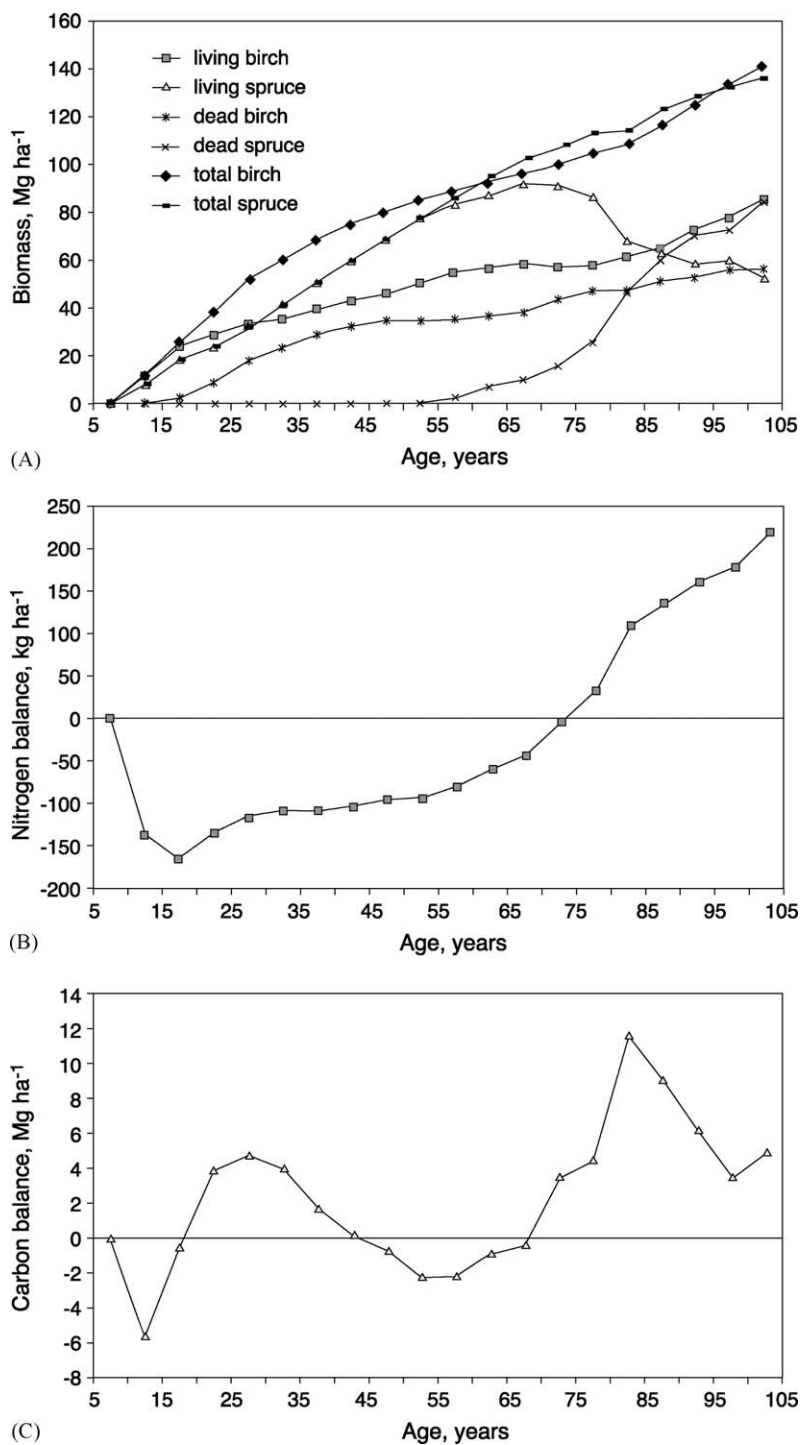| Timing of fellings	Pulp wood (m^3 ha^{-1})	Saw logs (m^3 ha^{-1})	Total timber (m^3 ha^{-1})	Logging residue (Mg ha^{-1})
Felling, year 15				
Norway spruce	–	–	–	–
Birch	5	–	5	14
Felling, year 40				
Norway spruce	25	–	25	10
Birch	52	–	52	8
Felling, year 60				
Norway spruce	42	–	42	9
Birch	–	–	–	–
Felling, year 80				
Norway spruce	20	30	50	9
Birch	–	–	–	–
Final felling, year 100				
Norway spruce	30	138	168	32
Birch	10	57	67	11
Total over 100 years				
Norway spruce	117	168	285	60
Birch	67	57	124	33
Norway spruce + birch	184	226	409	93

Fig. 7. Trends in (A) living and dead mass of stems and (B) nitrogen balance and (C) carbon balance of the soil system in a mixed Norway spruce–birch, *Betula pendula*, stand on a *Myrtillus* site in southern Finland.

age of 100 years. In the second, the thinning at the age of 40, 60, 80 years for spruce and the thinning at the age of 15 and 40 years for birch were done. In both cases, the final felling was done at the age of 100 years. In each thinning, 30% of the basal area of spruce and 50% of that of birch were removed. In the thinning, logging residues remained.

When thinnings were excluded, the biomass production for birch was higher only up to year 60, after which spruce grew more rapidly (Fig. 7). This implies, that the mortality of birch was quite high from the beginning of the simulation, whereas spruces began to die only after the year 55. The nitrogen balance in the soil was negative from the beginning of the simulation up to year 70, after which it increased up at about 230 kg ha^{-1} by year 100. The carbon balance for soil varied greatly following the mortality of trees, but it remained positive after year 65; i.e. at the end of the simulation there was 5 Mg ha^{-1} more carbon in the soil than at the beginning. Total timber production over the simulation was 34 m^3 ha^{-1} pulp wood and 96 m^3 ha^{-1} saw timber for birch and 42 and 56 m^3 ha^{-1} for spruce (Table 6).

When thinnings were applied the situation was slightly different; i.e. birch still grew faster in the early phase of the rotation but the overall growth for spruce was clearly higher than for birch. The mortality was quite same for both species throughout the simulation. Nitrogen balance for soil was negative up to the age of 50 years, after which it became positive and at the end nitrogen in the soil exceed by 270 kg ha^{-1} that at the beginning. Carbon balance in the soil varied also with the thinnings, but it was around the zero level throughout the simulation. Total timber production over the simulation was 67 m^3 ha^{-1} pulp wood and 57 m^3 ha^{-1} saw timber for birch and 116 and 169 m^3 ha^{-1} for spruce (Table 7).

5. Discussion and conclusions

This paper describes a model for computing the long-term succession of a population or a community of trees, together with the carbon and nitrogen turnover in a forested ecosystem. The model is an individual-based, spatially explicit one; i.e. trees are assumed to be located within the simulated plot in a grid of cells that are sufficiently small to contain not

more than one tree. Each tree consists of five compartments (stem, branches, leaves/needles, coarse roots and fine roots) and has its own nutrition area, which varies with time. Each tree competes with its nearest neighbours for available light and nitrogen. Tree growth is represented by calculating the growth due to light and the growth due to soil nitrogen and taking the smaller of these two values as the actual growth, following the law of Liebig (1843). The simulated plot has an explicit nitrogen–carbon balance based on the turnover of these elements in the ecosystem linked to the dynamics of organic matter in the soil. The model is in this respect a hybrid of several approaches needed to understand the dynamics of a forest ecosystem more thoroughly (Friend et al., 1997; Chertov et al., 1999a).

The basic philosophy behind the model is the same as that applying to many gap models (see Shugart, 1984); i.e. potential growth is limited by the availability of light and nitrogen, and by allowing for these, we obtain the actual growth. The potential growth referred to in this model is the potential biomass increment, represented by the integrating parameter of NPP in the form of the maximum possible biological productivity of leaves/needles, as presented by Chertov et al. (1999b). The response of a tree to the nitrogen supply in the soil is considered in terms of the specific consumption of nitrogen, i.e. the amount needed for the synthesis of one unit of mass.

Use is made of the spatially explicit distribution of trees in the stand for modelling the interaction between trees through the availability of nitrogen. The area from which a tree takes up nitrogen is dynamically related to the size of the tree, with the consequence that larger trees of the same species may eliminate smaller trees through competition for a limited nitrogen supply. This also holds good for competition between species, although differences in nutrient consumption may allow the coexistence of more than one species in the same stand.

The biomass increment is also dependent on the available light, and this procedure utilises shadowing mosaics in the stand, considered in relation to the species, sizes and locations of the trees. Furthermore, light limitation can affect the allocation of growth between height and diameter, implying that under conditions of light limitation, a tree will grow in height relatively more than in diameter. Similarly, given an ample supply of nitrogen, the radial growth will be

relatively greater than the height growth. The stem form will thus be modified in response to the supply of light and nitrogen. This feature of the model also makes it possible to study how the spacing of a tree stand and its management in terms of thinning may affect the predominant stem form and consequently the properties of the resultant timber. Stem properties are also affected by the procedure by which the total increment in a tree is allocated to different compartments, which is done here using species-specific proportions defined separately for three phases of maturity; i.e. taking into account the preference for the foliage in young trees, for the stem in more mature trees and for the roots in old trees. The interaction between these two procedures yields quite a realistic description of how the trees grow and develop with time in terms of the allocation of mass to their various compartments.

The mortality function used in the majority of gap models (Botkin et al., 1972; Shugart, 1984) uses a threshold value of diameter increment to determine dying tree. When tree has increment lower this threshold then it dies in 3 years. In this model, we yielded the same principle, but the threshold value for death is a proportion of leaf mass to total tree biomass as related to the total mass of the tree. If the current values of the ratio between the foliage mass and the total mass for a tree is less than the the threshold value, the tree will die. The threshold value for death is, thus not fixed but it depends on the total tree biomass; i.e. the higher is tree biomass the lower is the ratio; i.e. oppressed tree with low increment looses its leaf mass with increasing risk to die.

In general, the model yielded quite similar time courses for the main parameters of trees stands to those obtained from growth and yield tables and from the Finnish National Forest Inventory. It should be pointed out that the simulated growth curves are close to classic sigmoid-type ones for the growth of organisms (Shugart, 1984), and that comparison of the output from this model with that of two other models (Kellomäki et al., 1992, 1993) indicates that it succeeds quite well in simulating the growth of a population of trees representing different species throughout Finland. This makes it possible to study how management can interact with climatic and soil conditions to control the dynamics of tree populations and communities and the nitrogen and carbon turnover. The model can be also applied to the study of carbon sequestration in a forest ecosystem, with implications for the sustainable management of forest resources under boreal conditions.

References

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? J. Ecol. 84, 597–608.

Ågren, G.I., McMurtrie, R.E., Parton, W.J., Pastor, J., Shugart, H.H., 1991. State of the art of models of production decomposition linkages in conifer and grassland ecosystems. Ecol. Appl. 1, 118–138.

Alexeev, V.A., 1975. Light Regime of Forest. Nauka, Moscow, 228 pp. (in Russian).

Bartelink, H.H., 1998. Simulation of growth and competition in mixed stands of Douglas-fir and beech. Thesis. Landbouwuniversiteit, Wageningen, 222 pp.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Chertov, O.G., 1983a. The mathematical model of single plant ecosystem. J. Obshchey Biol. (J. Gen. Biol.) 44, 406–414 (in Russian with English abstract).

Chertov, O.G., 1983b. Quantitative approach to species ecological parameters with special reference to Scots pine (Pinus sylvestris L., Pinaceae). Bot. J. 68, 1318–1324 (in Russian with English abstract).

Chertov, O.G., 1990. SPECOM—a single tree model of pine stand/ raw humus soil ecosystem. Ecol. Modell. 50, 107–132.

Chertov, O.G., Komarov, A.S., 1997. SOMM: a model of soil organic matter dynamics. Ecol. Modell. 94, 177–189.

Chertov, O.G., Komarov, A.S., Karev, G.P., 1999a. Modern Approaches in Forest Ecosystem Modelling. Research Report N8. Leiden Boston Koln. Brill, European Forest Institute, pp. 1–130.

Chertov, O.G., Komarov, A.S., Tsiplianovsky, A.M., 1999b. A combined simulation model of Scots pine, Norway spruce and silver birch ecosystems in the European boreal zone. For. Ecol. Manage. 116, 189–206.

Chertov, O.G., Komarov, A.S., Tsiplianovsky, A.M., 1999c. Simulation of soil organic matter and nitrogen accumulation in Scots pine plantations on bare parent material using forest combined model EFIMOD. Plant Soil 213, 31–41.

Chertov, O.G., Komarov, A.S., Nadporozhskaya, M.A., Bykhovets, S.S., Zudin, S.L., 2001. ROMUL—model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modelling. Ecol. Modell. 138, 289–318.

Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based terrestrial biosphere model of ecosystem dynamics (Hybrid v 3.0). Ecol. Modell. 95, 249–287.

Karpov, V.G., 1969. Experimental Phytocoenology of Dark Coniferous Taiga. Nauka, Moscow, 350 pp.

Kazimirov, N.I., Volkov, A.D., Ziabchenko, S.S., Ivanchikov, A.A., Morozova, R.M., 1977. The Cycle of Elements and Energy in Pine Forests of Russian European North. Nauka, Moscow, 304 pp. (in Russian).

Kazimirov, N.I., Morozova, R.M., Kulikova, V.K., 1978. The Biomass and Elements Cycle in Birch Forests of Central Taiga. Nauka, Moscow, 216 pp. (in Russian).

Kellomäki, S., Kolström, M., 1994. The influence of climate change on the productivity of Scots pine, Norway spruce, Pendula birch and pubescent birch in southern and northern Finland. For. Ecol. Manage. 65, 201–217.

Kellomäki, S., Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U., Pajari, B., 1992. SIMA: a model for forest succession based on the carbon and nitrogen cycles with application to silvicultural management of the forest ecosystem. Silva Carelica 22, 85.

Kellomäki, S., Väisänen, H., Strandman, H., 1993. FinnFor: a model for calculating the response of the boreal forest ecosystem to climate changes. Research Note No. 6. Faculty of Forestry, University of Joensuu, Finland, 120 pp.

Killingbeck, K.T., 1996. Nutrients in senescent leaves: keys to the search for potential resorption proficiency. Ecology 77 (6), 1716–1727.

Koivisto, P., 1962. Kasvu-jatuottotaulukoita. Growth and yield tables. Commun. Inst. For. Fenn. 65 (8), 1–49.

Kolström, H., 1999. Ecological simulation model for studying diversity of stand structure in boreal forests. Ecol. Modell. 111, 17–36.

Kostin, N.V., 1997. Geographic variability of productivity of Norway spruce stands in European forest zone. PhD Thesis. St. Petersburg Forest Technical Academy (in Russian).

Kubin, E., 1983. Nutrients in the soil, ground vegetation and tree layer in an old spruce forest in northern Finland. Ann. Bot. Fenn. 20, 361–390.

Liebig, J.V., 1843. Die Chemie in ihrer Aswendung auf Agricultur und Physiologie. 5. Aufl. Braunschweig.

Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. For. Ecol. Manage. 73, 157–175.

Mälkönen, E., 1974. Annual primary production and nutrient cycles in some Scots pine stands. Commun. Inst. For. Fenn. 84 (5), 1–82.

Mälkönen, E., 1977. Annual primary production and nutrient cycle in a birch stand. Commun. Inst. For. Fenn. 91 (5), 1–28.

Marklund, L.G., 1988. Biomassafunktioner for tall, gran och bjork i Sverige. Summary: Biomass Functions for Pine, Spruce and Birch in Sweden. Report 45. Department of Forest Survey, Swedish University of Agricultural Sciences, p. 73 (in Swedish with English summary).

Rolff, C., Ågren, G., 1999. Predicting effects of different harvesting intensities with a model of nitrogen limited forest growth. Ecol. Modell. 118, 193–211.

Ryan, M.G., Hunt Jr., E.R., McMurtrie, R.E., Agren, G.I., Aber, J.D., Friend, A.D., Rastetter, E.B., Pullia, W.M., Raison, R.J., Linder, S., 1996. In: Breymeyer, A.I., Hall, D.O., Melillo, J.M., Agren, G.I. (Eds.), Comparing Models of Ecosystem Function for Temperate Conifer Forests. I. Model Descriptions and Validation. SCOPE 56-Global Change: Effects on Coniferous Forests and Grasslands. Wiley, Chichester, pp. 313–362.

Shugart, H.H., 1984. A Theory of Forest Dynamics. Springer, Berlin, 278 pp.

Tselniker, J.L., 1978. Physiological Basis of Trees Shade-Tolerance. Nauka, Moscow, 215 pp. (in Russian).

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. For. Ecol. Manage. 42, 95–110.

Vitousek, P., 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119 (4), 553–572.

Weishampel, J.F., Urban, D.L., 1996. Coupling a spatially explicit forest gap model with a 3D solar routine to simulate latitudinal effects. Ecol. Modell. 86, 101–111.